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Interactive comment on "Modeling seasonal and vertical habitats of planktonic foraminifera on a global scale" *by* Kerstin Kretschmer et al.

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Scientific significance: Excellent

The manuscript by Kretschmer et al. represents a substantial contribution to scientific progress within the scope of Biogeosciences. It is the latest one in a series of "foram-flux modelling" papers from the Bremen group. In 2006, Zaric et al. developed the first empirical model that described globally the fluxes of planktonic foraminifera at species level in dependence of sea-surface temperature, mixed-layer depth and export production. Over the years, the foram model itself, its parameterization, and its implementation and coupling to other models has evolved (e.g. Fraile et al., 2008; 2009; Kretschmer et al., 2016). The aim of all of these papers has always been to project the

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effect of changing environmental conditions on species distributional patterns in time and space. The current paper adds a vertical dimension to the existing foram model by applying the previously used spatial parameterization of biomass as a function of temperature, light, nutrition, and competition on depth-resolved parameter fields.

Scientific quality: good

The scientific approach and methods are valid. The results are discussed appropriately but the discussion lacks a critical analysis of the model-data comparison beyond the caveats mentioned in section 4.2 “Comparison with local observations”.

The authors write on p. 17 line 22-23: “This vertical migration of planktonic foraminifera during their ontogeny cannot be reproduced by PLAFOM2.0 as the model parameterizations do not include the individual species’ life cycles.”. It is quite understandable that implementing true reproduction cycles of cohorts of foraminifera, including “real” population dynamics and ontogenetic migration is beyond the present manuscript. Hence, the model does not calculate absolute or relative numbers of a certain species within a certain ontogenetic size class based on reproductive success and size specific growth- and mortality-rates, but rather calculates changes in species specific carbon concentration (in mmol C m$-$3), which can be converted to numbers afterwards.

There is nothing wrong with this approach but it means that the parameterization of PLAFOM2.0 is based on practical “sum” or “composite” parameters. These are then used to tune the model outcome to the overall data. For instance, growth of all species is approximated using a modified form of Michaelis-Menton kinetics in dependence of species specific food availability and temperature sensitivity (Fraile et al., 2008). To account for the light dependence with depth, influencing the growth of only symbiont bearing foraminifera, the authors included a “photosynthetic growth rate”. They use “. . .. . .a similar approach as Doney et al. (1996) and Geider et al. (1998), who determined phytoplankton growth rates by available light and nutrients. . ... (p.5 line 15-17)” . Such a parameterization is normally used for phytoplankton, that has orders of mag-

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nitude higher densities and cell division rates that respond very fast (within a day) and directly to light and nutrients. The symbiont bearing forams in this manuscript obey a (semi) lunar reproduction cycle and occur in densities that are very much lower, such that a "phytoplankton" kind of response cannot be expected. The authors use it as an additional tuning parameter for symbiont bearing forams next to food preference and temperature to develop species specific depth (light/nutrient) habitat preferences. Although it is a valid approach, the authors should clearly state that it is artificial.

Growth is balanced by mortality, which is not a formulation for "real" mortality but another tuning parameter: "we adjusted parts of the mortality rate equation to improve the model accuracy (p. 5 line 8-9).".

Overall, there are many factors that allow tuning, e.g. "p% represents the fraction of photosynthesis contributing to growth (p.5 line 31)". Interestingly, the authors have a higher p% for T. sacculifer (0.4) than for G. ruber (0.3), where I would have done it the other way around (see my comments on these species further below).

Another tuning factor is the temperature dependence of the predation term: ".....we followed Moore et al. (2004) and adjusted the temperature dependence of the predation term (MLpred in mmolCm−3s−1) (p.6 line 3-4). Also "....we included a stronger competitive behavior of G. bulloides by adjusting the free parameters in the competition term. (p.6 line 10-11). Having collected planktonic foraminifera by SCUBA diving for many, many years and looking at average typical blue water densities of ca. 10 specimens per m3 per species, and 3 dominant species in an assemblage, it is hard to believe that they compete with each other for resources as each of them occupies a space of only a few mm3 and they are stationary in the water column.

Certain boundary conditions also correct model misfits, e.g. "...zero fluxes have been replaced by half of the observed minimum flux. (p.7 line 25-26)".

All of these parameters were introduced to allow a good fit between model output and data but maybe not for the right reason. As such, we do not know how realistic this

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parameterization represents real planktonic foraminiferal population dynamics which is more complex (including lunar based reproduction cycles, ontogenetic migration, etc.).

Winter mixing, thermocline shoaling and annual irradiation changes are probably important parameters controlling foram population dynamics just as certain density layers may be important for gamete fusion in real foram life. I'm not sure how well these features are implemented in the models.

The bottom line is that, even though I appreciate the model and the manuscript a lot, I would like to see a discussion on these issues and if possible a statistical verification of the model performance. The description of the results and the discussion on modeled geographical ranges, seasonal and vertical distribution, as well as on the modeled seasonal variability of depth habitat, lacks a statistical treatment of the data. How good is the model performance and how sensitive is it to each of the model parameters?

I would appreciate a more quantitative treatment of the model performance instead of statements like "The predicted global distribution patterns of the five considered planktonic foraminiferal species are in good agreement with the core-top data (Figure 2) (p. 11 line 14-15)?

The discussion on the global distribution patterns is mostly related to temperature. What about the other parameters: food, nutrients, productivity, light, etc.? How does it compare to the "Longhurst Biogeographical Provinces". He partitioned the world oceans into provinces ("Ecological Geography of the Sea") based on the prevailing physical factors as a regulator of phytoplankton distribution, including temperature, photic depth, mixed layer depth etc. (e.g. Longhurst 1995; 1998).

Having "fixed" model parameters simulates so called "habitat tracking" of the forams through the seasons (but also on timescales of climate change or on glacial/interglacial cycles). This is a very important aspect to verify and would call for a section/paragraph by itself (see also Rebotim et al., 2017). For instance, on p15 line 23-25 you write "Rebotim et al. (2017) identified an annual cycle in the habitat of T. sacculifer and N.

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incompta in the subtropical eastern North Atlantic. Both species appear to descend in the water column from winter to spring and reach their deepest habitat in spring to summer before ascending again to a shallower depth towards winter (Rebotim et al., 2017).". How does this fit the "habitat tracking" picture? The authors could probably use observations on G. ruber and T. sacculifer for that as well. I may be wrong but I always thought that G. ruber lives closer to the surface than T. sacculifer (see also table 3 in Rebotim et al., 2017)? From laboratory experiments I know that T. sacculifer can handle living prey such as copepods much better than G. ruber while the latter seems to rely more on symbiont carbon, i.e. shows a more "autotrophic" lifestyle. Is it possible to see this in the data based on a more rigorous model-data comparison?

The results of the point-by-point comparative analysis for each site and species as provided in the Supplement (Figures S3 and S4) are very helpful but also show that the model is far from perfect and sometimes there is a complete mismatch. I would have appreciated a sensitivity study to determine the hierarchy of factors for the different species controlling the shell export fluxes regional and seasonal (including e.g. bimodal patterns) as well as the vertical distribution (including ALD). This would probably be a paper by itself but in my view a very important one.

Presentation quality: good/fair

Although the scientific results and conclusions are presented in a relatively clear and well-structured way it is not easy to grasp why the model underestimates e.g peak amplitude. What would happen if growth in the equation is increased or mortality is decreased? I sometimes wondered why the authors didn't play more with the model or used statistical techniques to quantify data-model mismatch (this is the reason for the "fair" mark). The number and quality of figures/tables is good and the supplementary material is very appropriate. The English language is very good.

Minor corrections:

On page 2 line 18-20: ". . . . . ..the lunar cycle and/or the structure of the water col-

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umn), which influence the species-specific depth habitats (including their mean living depth and vertical migration) (e.g., Fairbanks and Wiebe, 1980; Fairbanks et al., 1982; Schiebel et al., 2001; Simstich et al., 2003; Field, 2004; Salmon et al., 2015; Rebotim et al., 2017), the only attempt to model the vertical habitat is by Lombard et al. (2011).", and on page 17 line 20-23: "Several studies from different areas also showed that the main habitat depth of some species increases from the surface to deeper water layers during shell growth (Peeters and Brummer, 2002; Field, 2004; Iwasaki et al., 2017). Although I appreciate all the references that you list for ontogenetic migration and lunar cycle, there are only a few papers that specifically deal with very detailed population dynamics, lunar cyclicity and ontogenetic migration of planktonic forams that could/should be mentioned here (it was one of the first topics I studied when starting to work on planktonic foraminifera): Bijma et al., 1990; Bijma, 1991; Bijma and Hemleben, 1994; Bijma et al., 1994; Hemleben and Bijma, 1994; Schiebel et al., 1997. In my opinion, these references would fit best on p. 19 line 32-34: ". . .. .and by explicitly parameterizing the ontogeny of each individual planktonic foraminifera, thus, by considering the changes in the species' life cycles with depth, could considerably improve the model.".

P. 9 line 27-30: "Although seasonal changes in the modeled foraminiferal peak fluxes with temperature are evident, all five species exhibit an almost constant peak amplitude (i.e., the maximum concentration divided by the annual mean) in their preferred habitat, which is, i.a., limited by temperature. Outside their preferred living conditions the peak amplitudes increase for most of the species considerably (Figure 3).". It has not become clear to me what it means when "peak amplitude" is large or small in terms of real population dynamics ("bloom"?) and what it means in terms of model performance?

P. 14 line 26-28: "This would explain why the highest modeled concentrations of T. sacculifer occur at shallower depths compared to G. ruber (white) (see Figures 4d-e and 5d-e).". Striktly speaking this doesn't explain it because this is what you put into

the model in the first place (see my comments above)

P. 16 line 18: “G. bulloides, however, is found year-round close to the surface along the. . ...”. Write the genus name full at the beginning of a sentence.

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